THE EUGSTER GYNANDROMORPH BEES

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ABOUT fifty years ago von Siebold wrote his classic paper on "Zwitterbienen" in which he gave an account of anomalous bees that appeared in considerable numbers in a hive of a bee breeder, named Eugster, in Constance.[1] The particular interest that attached to the case was not only that a bee might be partly male and partly female, mixed in all manner of proportions, but that they were hybrid bees as well, the mother belonging to the race of Italian bees, while the father or fathers were German bees. Von Siebold did not state in his paper whether the male parts of the gynandromorph were like the father, or were hybrid, or were like the mother. In fact it was not until 1888 that the importance of such information was realized. In that year Boveri described a result that he had obtained with the eggs of the sea urchin, in which as a result of delayed fertilization (or of some irregularity in the penetration of the sperm into the egg) the sperm nucleus fused with one of the two nuclei resulting from the division of the egg nucleus. In consequence half of the nuclei were derived from the egg alone, while the other half of the nuclei arose from the union of the paternal and a maternal nucleus. If now, as other evidence seemed to show, one nucleus in the bee produces a male and two nuclei a female, such a partially fertilized egg should be male on one side and female on the other side of the body of the resulting individual. In this way, Boveri pointed out, the Eugster gynandromorphs might have arisen.

In 1905 I pointed out that the Eugster gynandromorphs might also be accounted for by means of another hypothesis. If two (or more) spermatozoa should enter the egg, one of them might unite with the egg nucleus while the

[1] Several earlier accounts of gynandromorph bees are extant (See "literature" list).

other might give rise to the nuclei of the rest of the embryo. On this hypothesis the combined nuclei would give rise to the female parts, while the single nucleus, here derived from the sperm, would give rise to the male parts. In support of such a view I pointed out that more than a single nucleus was known to enter the egg of the bee, and this condition has more recently been amply confirmed by Nachtsheim. I also pointed out, for the first time I believe, that a decision in favor of one or the other of these two hypotheses could be obtained if in these gynandromorph hybrids the nature of the male and of the female parts of the adult were known; for on Boveri's interpretation the male parts (derived from the single egg nucleus) should be maternal while on my view the male parts (derived from the single sperm nucleus) should be paternal. In both views the female parts of the gynandromorphs should be hybrid and therefore either intermediate in character or like the dominant strain.

Four years ago Professor Doflein looked through the collection at Munich, at the request of Boveri, to find out whether any of the Eugster bees were still preserved there, and luckily found a jar labelled "Apis Mellifica, Zwitterbienen" which turned out to be the bees that von Siebold had obtained. Owing to their long sojourn in alcohol the color was almost entirely gone and on the color depended the decision as to the difference between the two races that combined to produce the gynandromorphs. At first Boveri despaired of finding out from these alcoholic specimens whether the male parts were like the father or like the mother; but on cleaning the parts he found that he could still determine whether a part was more like the same part in one or in the other domesticated strain.

Briefly Boveri finds that the male parts of the gynandromorphs are maternal, while the female parts are paternal, which is the dominant character. This conclusion gives a decisive answer in favor of his hypothesis and sets my own aside for this case at least.

Boveri's evidence leaves no reasonable doubt as to the possibility of determining the nature of the character of

the gynandromorphs, yet the desirability of having it confirmed on living material may be still worth while, since, as Boveri points out in a postscript, von Engelhardt has recently (1914) described some hybrid gynandromorphs from fresh material which lead to the opposite conclusion from that to which Boveri has arrived. Von Engelhardt's bees arose from an Italian queen by a "domestic" drone. Until it is ascertained what variety was used as the domestic drone the value of the evidence is not entirely certain.

A student of Boveri's, Fr. Elsa Mehling, has made a very careful study of the Eugster gynandromorphs, paying attention to a number of characters. Her work adds many details of interest concerning the admixture of male and female parts, but does not, however, furnish much additional evidence concerning the origin of these parts. She arrives at the same conclusion as that reached by Boveri, viz., that the male parts are maternal.

In this connection it should be recalled that the long sought for evidence demonstrating that drones inherit the characters of their mother has at last been found by Newell. Working at an isolated station forty miles from Houston, Texas, he mated Italian and Carniolan races of bees. The Italians are distinctly yellow, while the Carniolans are more or less gray. The stocks used had been under observation for several generations and were known to be pure. When virgin Italian queens were mated to Carniolan drones the workers and queens (both of which come from fertilized eggs) are like the Italian yellow stock, which is, therefore, dominant as to color. The drones from this mating are also yellow, which is expected if they inherit from their mother, but the cross made this way is not decisive in regard to the inheritance of the drones, because the maternal color is here dominant. In the reciprocal cross the result is decisive. Thus when a Carniolan queen is mated to an Italian drone the workers and queens are yellow due to the dominant color of the father, but the drones are gray like the pure Carniolan drones. This result proves that the characters of the

drones come from the mother, which is in accord with Dzierzon's theory that the drones arise from unfertilized eggs. This is further established by the following evidence. The daughters (queens) that come from Italian queens by Carniolan drones give rise to two kinds of drones in equal numbers, viz., Italian and Carniolan, which is the expected result, since such daughters are hybrid and are expected to produce two kinds of eggs. Reciprocally also the daughters from Carniolan queens by Italian drones produce two kinds and only two kinds of drones in equal numbers. The result also shows that Mendel's law applies to the queen bee. Cuénot has recently recorded the appearance of some drones in hybrid hives that are intermediate or even like the father, but since the possible production of drones by hybrid workers was not excluded, at least so far as the published evidence goes, these sporadic cases can not be used to disprove the maternal inheritance of the drones.

Boveri has discussed certain cytological possibilities in relation to the gynandromorph bees that are of interest. His work, and that of Herbst on sea-urchin embryos, had shown that haploid nuclei have only half the volume of diploid nuclei. It might have been anticipated therefore that the nuclei (and cells) of the drone bee would be half the size of those of the queen or of the worker bee, but a study of the cells of drones by Oeninger had already shown that their nuclei are as large as are those of the workers which have the diploid number of chromosomes. It is not possible therefore to determine by microscopic study of nuclear size whether or not the male parts of gynandromorphs come from a single nucleus.

Boveri points out that, since the nucleus of the egg of the bee, if not fertilized, proceeds to divide, it is improbable that the division center is brought in by the sperm, as appears to be the case in so many other eggs. Nachtsheim's observations confirm, he believes, this interpretation in the bee; for, according to Nachtsheim, three to seven or more nuclei enter but only one of these fuses with the egg nucleus. The others move out into the egg,

their chromosomes are resolved, and a spindle develops. But these spindles lack centrioles at their poles. The mitotic figure that has reached this stage then proceeds to degenerate. The absence of the centrioles indicates, Boveri thinks, that the spermatozoa of the bee does not bring in a division center, hence this cell organ must be contributed by the egg, and in consequence we can now easily understand how facultative parthenogenesis is, so to speak, a normal phenomenon in this egg. Boveri does not point out however that Nachtsheim's figures show that the polar spindles of the bee's egg also lack centrioles, and yet mitotic division is accomplished. It seems highly questionable therefore whether much weight is to be attached to the absence of centrioles in the supernumerary sperm figures. The chief interest that attaches to Boveri's argument is his disclaimer that he intended his striking statement in regard to fertilization, namely, that the sperm furnishes the dynamic division center for development, to be taken as a universal dictum. The incitement of artificial division centers in such eggs as those of the sea urchin in which the sperm brings in the centriole (or causes its development in the immediate vicinity of the sperm nucleus) shows how little importance can be attached to the hypothesis of the genetic continuity of the centrosome. If in the case of the bee three or more sperm enter each egg all bees would be gynandromorphs should all the sperm develop. Obviously, some special condition must be assumed to be present if these sperms are to go forward and complete their development which they begin even under ordinary circumstances. Boveri himself must also invoke some special condition, such as retarded fertilization, in order that one of the entering sperm fuses with one of the products of the first division of the egg nucleus. It might equally well be postulated that delay in the fertilization and the consequent impetus to parthenogenesis might be favorable for the completion of the division of the supernumerary asters. In a word it is doubtful if Boveri's interpretation gains much from his cytological argument. If his observations on the dis-

tribution of color are well established this further argument is superfluous.

In 1906 Toyama described a gynandromorph that arose when two races of silkworm moths were crossed. From an analysis of the genetic evidence I pointed out that in this case the male parts of the gynandromorph must have been paternal and the hybrid parts maternal (dominant). If the same conditions prevail here as in the bee, viz., one nucleus producing a male and two producing a female,[2] the case is in harmony with my hypothesis and not with that of Boveri. But the evidence for my view is not as strong as that Boveri's is now for the bee; yet it may be true, nevertheless, that in both of these ways gynandromorphs may arise. A third mode of origin has been shown, from the genetic evidence, to apply to *Drosophila,* viz., dislocation during ontogeny of the two sex chromosomes. In fact we should expect that gynandromorphs would arise in insects whenever certain nuclei come to contain two sex chromosomes and others only one. The means by which this segregation takes place may differ under different conditions.

Goldschmidt has recently explained the remarkable gynandromorphs that he obtains in crosses between *Lymantria dispar* and *L. japonica* in still a different way, one that involves the relative potencies of the sex factors in the different races.

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[2] Whether one is justified in applying to the case of the moth the hypothesis for the bee may be seriously questioned because in the case of the moth the male is assumed to be the result of one sex chromosome (*z*) in conjunction with the *haploid* number of autosomes, while in the female moth one sex chromosome (*z*) and its mate (*w*) (which from Doncaster's evidence has no sex-determining influence) in conjunction with the *diploid* number of autosomes is assumed to stand for the female soma.

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